EFFECTS OF PATCH SIZE AND HABITAT STRUCTURE ON THE MOVEMENTS OF ADULT MALE WOOD TURTLES, *GLYPTEMYS INSCULPTA*

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Abstract.—Populations of the North American Wood Turtle (*Glyptemys insculpta*) are often encountered in agricultural landscapes. We used thread-trailing techniques to record the movements of six adult male *G. insculpta* translocated to an experimental hayfield patch-matrix. We investigated the effects of patch size and habitat structure on path sinuosity, turning angles, and move length. Paths confirm the occurrence of three movement phases previously described in other animals: agitation dispersal, local search, and ranging. Within-patch movements revealed a left-turning bias that was not the result of a serial autocorrelation of turning angles. We propose that the arced paths observed are a result of handedness and/or diagonal sequence gait. As patch size had no effect on path sinuosity or move length, our results demonstrate the consistency of path characteristics within hayfield patches up to 30 m in diameter. Local search was characterized by a unidirectional series of zigzag moves. Habitat structure affected path sinuosity and move length. Generally, paths were straighter and move lengths longer in the harvested area. These results are consistent with the findings of studies on small mammals and insects moving through exposed or resource-poor areas. Boundary permeability was absolute, with all subjects crossing patch perimeters without any hesitation in movement. Translocated *G. insculpta* exhibit predetermined search phenotypes, and move to maximize the likelihood of locating resources, while minimizing the probability of revisiting previously searched areas.

Key Words.-Glyptemys insculpta; habitat structure; haying; movements; patch size; sinuosity; spatial ecology; translocation

INTRODUCTION

Knowledge of wildlife movement patterns within fragmented ecosystems is essential for the success of conservation efforts (Taylor et al. 1993; Harrison and Fahrig 1995). Since the early 17th century, deforestation has resulted in the loss of an estimated 160 million ha of natural forest in temperate North America (Goudie 1990). Since 1994, Canada alone has harvested over one million ha of forest per year (Environment Canada 2003). For threatened and endangered species exposed to such exogenous disturbances (i.e., of recent, often human-induced, origin), a detailed understanding of landscape connectivity is vital. Taylor et al. (1993) defined landscape connectivity as "the degree to which the landscape facilitates or impedes movement among resource patches."

One particularly well-suited organism for experimental studies on the effects of exogenous landscape alterations is the North American Wood Turtle, *Glyptemys insculpta* (Garber and Burger 1995). *Glyptemys insculpta* are semi-aquatic riparian obligates that range widely throughout the northeastern United States and Canada (Harding and Bloomer 1979). They are a disturbance-dependent species, requiring openings

in the forest canopy for foraging, thermoregulation, and incubation of eggs (Harding and Bloomer 1979; Compton et al. 2002; Walde et al. 2007). Thus, *G. insculpta* are often encountered in agricultural landscapes, with individuals frequenting pastures, hayfields, and other croplands such as cornfields (Kaufmann 1992; Niederberger and Seidel 1999; Ernst 2001; Saumure et al. 2007; Tingley et al. 2009). However, movement within these habitats exposes *G. insculpta* to agricultural machinery, which results in unsustainable levels of mutilation and mortality (Saumure and Bider 1998; Daigle and Jutras 2005; Saumure et al. 2007; Tingley et al. 2009).

The lack of research specifically addressing the effects of patch size and habitat structure on turtle movements has prompted us to examine how such landscape variables affect the movement patterns of *G. insculpta*. An agricultural patch-matrix design was deemed most appropriate due to: (1) the prevalence of hayfields throughout the species' range; (2) the documented use of hayfields by *G. insculpta*; and (3) the high mortality and mutilation rates documented therein. The objectives of our study were twofold. Firstly, to ascertain whether adult male *G. insculpta* translocated to a hayfield patchmatrix exhibit discernable movement patterns.

Secondly, to determine the effects of habitat structure and patch size on path sinuosity, turning angle, and move length (*sensu* Turchin 1998). We hypothesized that *G. insculpta* path characteristics were independent of patch size and habitat structure (i.e., patch vs. matrix).

MATERIALS AND METHODS

Subjects .- We obtained Wood Turtles from an agricultural site in southern Québec from 20 July to 15 August, 2000. This source population has been described in detail elsewhere (Daigle 1997; Saumure and Bider 1998; Daigle and Jutras 2005; Saumure et al. 2007). Our experiment was conducted with similarsized adult male subjects only, thus eliminating morphological and intersexual effects. Current theory suggests that males frequently have enhanced spatial abilities as a result of greater mobility (Gaulin and FitzGerald 1989; Gibbons et al. 1990; Williams et al. 1990; Roof and Havens 1992). Moreover, males are known to spend more time in agricultural fields than females (e.g., Tingley et al. 2009). We excluded turtles with potentially debilitating injuries, as amputations can affect path length, sinuosity, and turning angles (Claussen et al. 1997).

Study site.—We translocated turtles approximately 100 km NW to two contiguous hayfields comprised of 6.2 ha at the Macdonald Campus Farm Field Unit of McGill University in Ste-Anne-de-Bellevue, Québec, Canada. Both hayfields were composed of a mixture of Smooth Brome (*Bromus inermis*) and Reed Canary (*Phalaris arundinacea*) grasses. The hayfields also contained Cow Vetch (*Vicia cracca*) and scattered Common Milkweed (*Asclepias syriaca*). We considered the fields quasihomogeneous, which is defined as a scale of plant heterogeneity that is less than the scale of the subject's dispersal (Turchin 1998). At the onset of experimentation, hay height varied from approximately 0.66–1.00 m.

Techniques.—Dense vegetation invariably hampers the sighting, and thus capture, of turtles in mid-summer (Lovich et al. 1992). However, our subjects were captured readily because they had been equipped with radio-telemetry transmitters as part of a previous study (Saumure et al. 2007). At the onset of experimentation, we captured turtles at the agricultural site and held them temporarily in large cotton bags during field transport. We transferred subjects to large 68 L Rubbermaid[®] containers upon reaching a vehicle. Each container was filled with water, to a depth of approximately 5 cm, to ensure that subjects were hydrated. We then transported the turtles to the experimental site. The following day, we equipped subjects with a thread-trailing device (Breder 1927; Schwartz and Schwartz 1974) and

released them in the experimental arena. We released subjects at ~ 0800 h on sunny days with varying degrees of cloud cover: no releases occurred on completely overcast or rainy days. Previous research has demonstrated that thread-trailers do not significantly affect the movements of Eastern Box Turtles (Terrapene c. carolina), a smaller terrestrial species (Stickel 1950). We used a thread-trailer model that was very similar to that of Claussen et al. (1997). Different colors of thread were used for each turtle to avoid confusion during data recording. We compiled thread-trail data at the conclusion of the experiment rather than after each set of trials, as the act of mapping the paths could seriously disturb the structure of the havfield. At the conclusion of the two 24-h trials, we removed thread-trailers and transmitters and we returned turtles within 48-h to their respective points of origin within the source population. Our mapping procedures were similar to those of Claussen et al. (1997); we gathered the data with a compass and meter stick. Paths were graphed using ArcView[®] GIS software (Environmental Systems Research Institute, Inc., Redlands, California, USA).

experiment.—We designed the patch Patch experiment to determine the importance of patch size and habitat structure on the fine-scale movements of G. insculpta. Patches are defined as areas with relatively high probability of encountering resources surrounded by areas where the probability is essentially nil (Bell 1991). This latter non-habitat area is classically referred to as 'the matrix' and is characterized by low structural complexity (Wiens 1995). We released turtles in the center of two circular patches (one 30 m diameter, one 15 m diameter) of uncut hayfield surrounded by a harvested area, i.e., the matrix. A circular shape was chosen to ensure a constant radial distance to the patch perimeter, enabling comparisons of movements in any direction. The 30 m diameter patch was the largest that could be created while still leaving ≥ 8 m of mowed matrix.

We placed turtles in each patch for one experimental trial. To limit the effects of prior exposure, we randomly assigned turtles to their initial patch. Trials began by placing a turtle equipped with a thread-trailer at the center of each patch. We then permitted subjects to move undisturbed for 24 h. Choice of this time period reflected: (1) thread spool length limitations; (2) patch sizes; and (3) known mean displacement of 108 ± 90 m per 24-h period (Strang 1983). We staked path end points and marked them with flagging tape at the end of each trial. A move is defined as "a segment of a path between two consecutive stopping points" (Turchin 1998); thus, move length is simply the length of a given path segment.

Saumure et al.—Habitat effects on movements of male Wood Turtles.



FIGURE 1. Paths of six adult male *Glyptemys insculpta* within and beyond a 15 m diameter hayfield path-matrix. The perimeter of the hay patch is indicated by the circle.

Data analyses.--We analyzed Glyptemys insculpta paths by several statistical methods. We estimated sinuosity by the ratio of d/L; where d is the greatest distance between any two points on a given path, and L is the total path length. This index produces a numerical value ranging from 0 to 1, with increasing values indicating straighter paths. This measure of sinuosity is particularly suited for the analyses of paths of homing and/or transient animals (Claussen et al. 1997). When comparing the effects of habitat structure (i.e., patch vs. matrix) on path sinuosity, we used a constant L value, as recommended by Claussen et al. (1997). As a result, in most cases we used only a portion of the path data beyond the perimeter of each patch. This portion of path corresponded exactly to the length of the path laid down within the un-mowed patch. We compared sinuosity and move length data using paired-sample *t*-tests.

We calculated turning bias in the initial five postrelease moves *a posteriori*. To calculate turning bias, we designated right and left turning angles as positive and negative, respectively. We summed these signed turning angles and calculated their means (Bell 1991). Contingency tables for analyses of overall directional biases in turning angles were analyzed with the adjusted G-tests of independence (G_{adj}) using William's correction (Sokal and Rohlf 1995; Turchin 1998). We accomplished common statistical analyses using version 10 of SYSTAT[®] (SPSS Inc., Chicago, Illinois, USA). Statistical tests were set at $\alpha = 0.05$.

RESULTS

Subjects.—We obtained six adult male *G. insculpta* of similar size from the source population for our experimental trials. Mean measurements, expressed as mean \pm SD (range), were: Carapace Length = 197.8 \pm 3.10 mm (193.8–201.9 mm); Carapace Width = 148.5 \pm 4.54 mm (141.9–154.1 mm); Plastron Length = 176.9 \pm 4.62 mm (171.7–184.0 mm); Mass = 1104.2 \pm 29.2 g (1075–1150 g). The precise age of each subject was unknown (Saumure and Bider 1998).



FIGURE 2. Paths of six adult male *Glyptemys insculpta* within and beyond a 30 m diameter hayfield path-matrix. The perimeter of the hay patch is indicated by the circle.

Analysis of movements.—Most paths were characterized by an initial series of relatively short moves that produced an arc away from the release point (Figs. 1, 2). Note that subjects did not follow our paths to and from the center of each patch; nor did they follow each other's paths (Figs. 1, 2). A *posteriori* examination of initial turning bias (i.e., the first five moves) revealed a negative (left) turning bias in 8 of 11 (72.7%) of the paths (Table 1). One perfectly straight path was excluded from turning bias calculations. Although there

were significantly more left turns within patches (right:left = 0.705:1, N = 133, $X^2 = 3.98$, P < 0.05; Fig. 3), there was no significant difference in turning frequencies for moves beyond the patches (right:left = 0.724:1, N = 50, $X^2 = 1.28$, P > 0.05; Fig. 4). However, a comprehensive analysis of all turning angles within the 15 and 30 m patches revealed an absence of 1st order serial autocorrelations (*sensu* Turchin 1998) in turning angles ($G_{adj} = 2.36$, P > 0.05). Moves beyond the two patches were also sequentially independent ($G_{adj} = 0.50$,

TABLE 1. Initial bias in right (+) and left (-) turning angles of adult male Glyptemys insculpta moving away from a central release point within 15 m and 30 m diameter havfield patches. An asterisk (*) indicates that the turtle was randomly selected to undergo the first trial in the 15 m patch.

Turtle #	15 m patch	30 m patch
2	- 37.4°	- 12.0°
15	+ 6.4°	- 4.6°
25*	no bias	+ 14.2°
102*	- 32.0°	- 27.2°
111	- 12.4°	- 51.8°
119*	- 14.2°	+ 1.4°

P > 0.05). Interestingly, turning angles within patches 0.950; Table 3). were as wide as 150° (Fig. 3); whereas, those in the matrix only reached 120° (Fig. 4). We observed that the arced portions of paths ended abruptly and were followed by a series of unidirectional zigzag moves. None of the turtles chose to remain within the experimental patches and none crossed their own paths during a trial.

Structural complexity.—We compared path sinuosity for movements within and beyond the perimeter of 15 m and 30 m un-mowed havfield patches (Table 2). A definite trend towards straighter paths beyond the perimeter of the 15 m patch was detected (t = -2.371, P =0.064). Paths beyond the perimeter of the 30 m patch were significantly straighter than those within (t = -8.865, P = 0.001). Mean move lengths within vs. beyond the 15 m patch did not differ significantly (t = -1.792, P = 0.133; Table 3). Conversely, mean move lengths made beyond the 30 m patch were significantly longer than those within it (t = -5.022, P = 0.004; Table 3).

Patch size .-- Fine-scale movements of each turtle were plotted (Figs. 1, 2). A comparison of within-patch sinuosity (d/L) between 15 m and 30 m patches revealed no significant difference (t = 1.081, P = 0.329; Table 2). Moreover, no differences were detected in path sinuosity beyond the perimeter of the two patches (t = 0.562, P =0.598; Table 2). A comparison of mean lengths for moves within the 15 and 30 m patches revealed no significant differences (t = 0.749, P = 0.488; Table 3). Similarly, no differences in mean lengths for moves beyond the two patches were detected (t = -0.066, P =

DISCUSSION

The paths we observed can be classified into three previously described movement phases: (1) agitation dispersal; (2) local search; and (3) ranging (Bell 1991; Turchin 1998). Herein, we define agitation dispersal as innate movement in response to a stressor (i.e., a classic flight response). Agitation dispersal manifested itself as an arc in the initial post-release path of a given G. insculpta (Figs. 1, 2). Such post-release arcs have been noted during other studies of G. insculpta (Barzilay 1980; McCurdy 1995). Barzilay (1980) suggested that the arcs resulted from initial periods of disorientation in unfamiliar environments. McCurdy (1995), however, disputed the disorientation hypothesis because his subjects had not been translocated, and were thus still within their activity areas. Rather, he interpreted arcs as an initial flight followed by topographic orientation Our interpretation that taxis is a (Jander 1975). of manifestation agitation dispersal, however, corroborates both of the aforementioned theories: an innate flight response precludes orientation, where orientation is defined as the mechanism responsible for the recognition and maintenance of direction (Bell 1991). Cabanac and Bernieri (2000) recently demonstrated that, despite appearances, G. insculpta experience tachycardia as a result of even short-term Researchers desiring to reduce gentle handling. agitation dispersal movements might benefit from using the release method described in Yeomans (1995). This method uses a rudimentary pulley system to release subjects from beneath buckets after a predetermined

TABLE 2. Path sinuosity (d/L) of adult male *Glyptemys insculpta* moving within and beyond the perimeter of 15 m and 30 m diameter un-mowed hayfield patches. An asterisk (*) indicates turtles that were randomly selected to undergo the first trial in the 15 m patch.

	15 m patch		30 m	patch
Turtle #	Within	Beyond	Within	Beyond
2	0.745	0.929	0.833	
15	0.864	0.990	0.887	0.995
25^{*}	0.995	1.000	0.368	0.510
102^{*}	0.801	0.963	0.806	0.976
111	0.892	0.836	0.617	0.832
119*	0.611	0.746	0.659	0.849





FIGURE 3. Frequency of right (+) and left (-) turning angles of six adult male *Glyptemys insculpta* moving within 15 m and 30 m hayfield patches.

period.

Our analyses of path turning characteristics revealed that turtles exhibited a left turning bias within patches (Fig. 3). Moreover, this bias was real and not the result of serial autocorrelations in turning angles. Casteel (1911) first described the development of right or left turning bias in Painted Turtles (Chrysemys picta) used in behavioral experiments that employed mild electric shock as negative reinforcement. The shock, or anticipation thereof, might be sufficient to result in the expression of an innate movement bias. Subsequent research on the same species, but without electrical stimulation, did not detect any turning bias (Ortleb and Sexton 1964). Claussen et al. (1997) did not detect a turning bias in the paths of in situ Ornate Box Turtle, Terrapene ornata. Similarly, little evidence for turning bias was observed in foraging juvenile Gopher Tortoises, Gopherus polyphemus (Halstead et al. 2007). Intuitively, a bias in taxis must result from a series of asymmetrical movements. During agitation dispersal. innate biases in gait are expressed. We propose two mechanisms, acting alone or in combination, that may account for such results. Firstly, in situ G. insculpta exhibit 'handedness' (unpubl. data), a phenomenon recorded previously in frogs, lizards, and even snakes (Dill 1977; Willard 1977; Deckel 1995; Oseen et al. 2001; Roth 2003). This is perhaps not surprising given the ability of G. insculpta to manipulate food with their forelimbs (Carr 1952; Babcock 1971; Harding and Bloomer 1979). Behavioral asymmetry is thought to be a result of hemispheric specialization, a tangible expression of the lateralization of the nervous system (McKeever 1991). Recent research has found that turtles have shared neural circuitry for two non-related

FIGURE 4. Frequency of right (+) and left (-) turning angles of six adult male *Glyptemys insculpta* moving through the matrix beyond 15 m and 30 m hayfield patches.

functions (i.e., scratching and swimming), which suggests other movements may also be linked (Berkowitz 2002). Secondly, G. insculpta are the only species of turtle known to possess a diagonal sequence gait (Hildebrand 1966; Zug 1971; pers. obs.). Gait has been shown to influence the fine-scale paths of cockroaches (Bell 1991; Turchin 1998). Once physiological stress responses have abated, G. insculpta enter a local search phase. Transition between the first two movement phases is quite pronounced (Figs. 1, 2). Glyptemys insculpta movements during the local search phase were characterized primarily by unidirectional series of zigzag moves. Similar unidirectional movements have also been observed in homing experiments with the terrestrial Eastern Box Turtle (Lemkau 1970). Zigzagging is thought to be a mode of movement used when physical orientation cues are absent (Bell 1991; Andreassen et al. 1996a). Additionally, it is likely to be more effective at producing forward movement than attempting to move in a perfectly straight line (Bell 1991). Functionally, zigzag movements may have been the result of: (1) deflection by the patchy distribution of hay stems (Goodwin and Fahrig 2002); (2) visual obstruction produced by the vertical structure of a mature hay crop; and (3) an artifact of gait (Bell 1991; Turchin 1998). However, one G. insculpta (# 25, Fig.1) transected the radius of the 15 m patch without deviation or deflection, regardless of the structural complexity of the intervening vegetation (Fig. 1). This individual may simply have bypassed the agitation dispersal phase of movement. Intraspecific differences in post-handling behavior have long been recognized in turtles (e.g., Casteel 1911; Gould 1957; Belinky and Belinky 1974). Thus, it is not

		15 m patch				30 m patch		
Turtle #	N	Within (cm)	Ν	Beyond (cm)	N	Within (cm)	Ν	Beyond (cm)
2	15	75.8	7	165.1	9	200.0	1	555.0
15	8	123.5	3	316.0	12	134.1	2	862.0
25	1	745.0	1	1,150.0	22	190.9	7	565.3
102	8	153.7	1	1,210.0	21	81.0	5	430.6
111	6	148.7	5	182.0	15	231.7	7	384.0
119	7	181.7	8	169.4	17	139.5	8	485.2

TABLE 3. Mean length of moves for adult male *Glyptemys insculpta* moving within and beyond the perimeter of 15 m and 30 m diameter hayfield patches. Number of moves indicated by N.

surprising that turtle # 25, as well as another specimen, began two additional paths in the local search phase (# 119, Fig. 1; # 25, Fig. 2). Although these paths comprised seemingly broad arcs, a closer examination reveals that these 'arcs' each contained a series of unidirectional zigzag movements, but in two different directions. In these cases, handling stress may not have resulted in flight, but rather in the chelonian 'refuge strategy' (i.e., withdrawal into relative safety of the shell). Once the stress had abated, the turtles then became active. Tinklepaugh (1932) observed that a male G. insculpta withdrew for periods ranging from minutes to hours. Direct observations of G. insculpta movements during further experiments may reveal how turtles react to perceived threats. If G. insculpta do not flee a rapidly approaching disc mower, for instance, such inaction may have fatal consequences and thus, direct conservation implications. Such information is particularly relevant because the source population, from which our turtles originated, experiences extremely high mortality and mutilation rates (Saumure and Bider 1998; Daigle and Jutras 2005: Saumure et al. 2007).

Our results are consistent with the null hypothesis that path characteristics of adult male G. insculpta are independent of patch size. One could argue that an insufficient difference existed between the two patch diameters to elicit a change in search strategies. Animals in unfamiliar areas, however, move to maximize the likelihood of locating resources, while minimizing the probability of revisiting previously searched areas (Bell 1991). This is precisely what we observed, as none of our subjects crossed their own paths and both patches were evacuated within the 24 hour trial periods. In the absence of information on patch size, our translocated turtles probably defaulted to predetermined search phenotypes. Our results demonstrate the consistency of path characteristics within quasihomogeneous patches up to 30 m in diameter. Such a patch represents a diameter 150 times that of the mean CL of our subjects. This scale is consistent with the distance G. insculpta will venture away from 'edge' habitats into hayfields in agricultural areas (Tuttle 1996; unpubl. data).

Bell (1991) defined 'ranging' as movements beyond a patch or resource while in search of another, regardless

of the orientation mechanism used. Ranging is characterized by a decrease in local search movements (sensu Bell 1991) and an increase in linear displacement. Current theory suggests that changes in habitat structure will produce noticeable changes in movement patterns of animals (Wiens et al. 1985; Bell 1991). Indeed, our data refute the null hypothesis that path characteristics of adult male G. insculpta are independent of structural complexity. When we compared paths within and beyond the 30 m patch, paths through the mowed matrix were straighter and mean move lengths were longer. Although a similar trend was observed in the 15 m patch trials, the lack of statistical significance may be attributed to limitations imposed by the patch size itself. Specifically, sample sizes (i.e., number of moves) were fewer because turtles required fewer moves to reach the patch perimeter. Nonetheless, a behavioral response to the change in habitat structure was observed. Voles, snakes, and insects have also been shown to exhibit changes in movement patterns when crossing through exposed or resource-poor habitats (Heinrich 1979; Tiebout and Cary 1987; Andreassen et al. 1996b; Gillis and Nams 1998; Berggren et al. 2002). Given that ranging can be interpreted as a form of area-avoidance behavior, recently harvested hayfields can be viewed then as a 'temporal matrix'. Researchers have only just begun to investigate the effects of temporal variability on landscape connectivity in agricultural landscapes (Baudry et al. 2003).

Our findings demonstrate that translocated adult male *G. insculpta* venture into, and cross, a harvested hayfield despite the presence of a high boundary contrast, or 'hard edge.' Moreover, the absence of back-tracking or deflection at patch perimeters indicates that this occurs without any hesitation (Fig. 1, 2). Thus, the boundary permeability of our experimental hayfield patch-matrix was 100%. Given that boundary permeability was absolute, one might suggest that *G. insculpta* do not regard the mowed hayfield as a non-habitat matrix. However, the combination of straighter paths, longer moves, and observations of turtles *in situ* (Saumure et al. 2007) indicate otherwise.

Typically, organisms that are foraging successfully perform large dimension turns when they encounter a patch border (Bell 1991). This implies that *G. insculpta*

patches. Moreover, our initial handling and presence likely inhibited foraging (Hassell and Southwood 1978). We believe that our translocated subjects were exhibiting predator-avoidance behavior. Although handling G. insculpta may have induced the movement patterns we observed, prior experience may have also been a factor. The G. insculpta used in our experiment had survived biannual having operations unscathed. In situ G. insculpta have been observed to evacuate hayfields at the onset of having (Saumure et al. 2007). Although neither the auditory cues nor the ground vibrations emanating from mowing machinery in close proximity were present during our experimental trials, G. insculpta may have detected the distinct odor of cut hay. Barzilay (1980), using anosmic and control animals, found that G. insculpta rely primarily on their sense of smell to home. Olfaction appears to be well developed and an important cue in the movements of several turtle species (Chelazzi and Delfino 1986; Graham et al. 1996; Quinn and Graves 1998). Thus, we suspect that prior experience with agricultural machinery rendered our subjects highly motivated to evacuate our experimental patch-matrix.

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